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Allochthonous ecosystems - ecosystems without producers

Abstract

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Allochthonous ecosystems occur under extreme conditions which do not allow the growth of green plants. They are lacking in producers, in diaspore banks, and in herbivores. Allochthonous ecosystems are best known from extreme deserts.
Two examples from the E Sahara (SW Egypt) are discussed. Here the completely vegetationless area is surrounded by a belt of accidental vegetation (in the sense of Kassas 1952) which is almost exclusively dependent on rainfall and duration of water resources. Since precipitations events do not take place annually but in much longer periods (if any) an annual rhythm does not exist. The life form of a typical member of accidental vegetation is neither annual nor therophytic, and it only facultatively carries out a perennial life cycle. For this life form the new term "poikilorhythmic" is proposed.

Introduction

Many decades of years since Odum's "Fundamentals of ecology" (Odum 1959) ecosystem studies revealed that the elementary characteristics of ecosystems like biocoenosis and habitat/biotope, food chain/food web, matter cycling and energy flow can be applied in a very general way to ecosystem structures and processes. But it has also been shown that a great variety of quantitative and qualitative peculiarities occurs in different ecosystem types. One of the most remarkable features is the existence of ecosystems lacking in producers which has been worked out first in deserts (Walter 1973). These ecosystems are completely carbon allochthonous and, thus, can be called allochthonous ecosystems (Bornkamm 1987a). Since this phenomenon has not yet been recognized sufficiently in ecology, in the present paper allochthonous ecosystems shall be characterized and the transition into the surrounding vegetation, included the life forms of plants involved in this transition, shall be discussed. The scientific plant names used in the paper follow Boulos (1995).

Characterization of allochthonous ecosystems

Walter (1973, 1975, 1986) described dune areas in the Namib Desert which are void of vegetation but showed a rich, and highly endemic, fauna (Kühnelt 1965, 1976). Under the viewpoint of ecosystem structure Walter (1973) used the terms " dependent ecosystems" resp. " natural terrestrial ecosystems without producers" (Walter 1975). Bornkamm (1987a) described large areas in the Eastern Sahara (SW Egypt) which were free of present vegetation and furthermore did not show any traces of former recent vegetation where, however, animal life could be detected (although was not investigated closely, see also Bornkamm & Kehl 1990).

In Fig. 1a a scheme is shown for the ecological functions in typical complete (autochthonous) ecosystems, whereas Fig. 1b applies to allochthonous ecosystems. Here, since producers do not exist true herbivores are not occuring either. It is evident that allochthonous ecosystems are incomplete regarding the biological components but they still show some of the characteristic ecosystem processes like short food chains, some matter cycling and a kind of energy flow.

The concept of allochthonous ecosystems can be applied to quite a number of different ecological situations. In deserts lack of water is the overriding factor for the absence of vegetation but the same result can be achieved by lack of light (e.g. in caves), by mechanical reasons (e.g. in buildings), lack of nutrients (e.g. in combination with heat in young lava flows), presence of toxic substances or strong radiation. These examples differ wide-

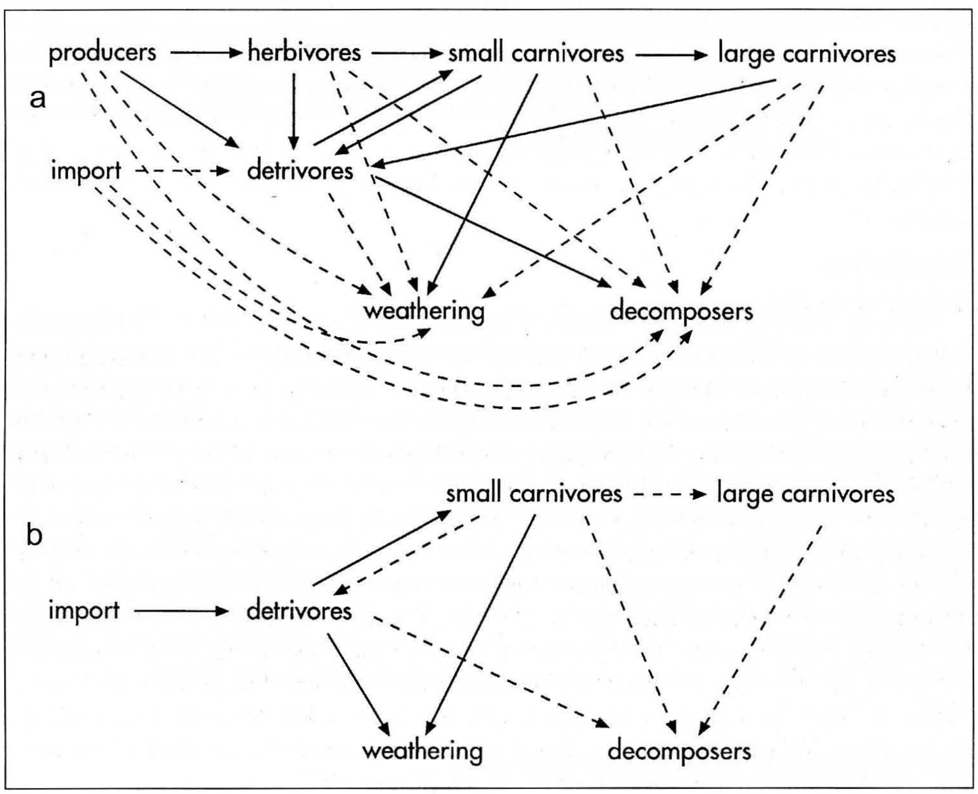

Fig. 1. Functional relationships in a complete (autochthonous) ecosystem (above), and in an allochthonous ecosystem (below). Solid lines = main processes, dotted lines = subordinate processes.

ly in spatial and temporal scale, and not always just one crucial factor can be found to be responsible for the lack of producers. In the Namib dunes with appr. 10 mm of average annual precipitation at least from time to time the emergence of a few plants seems possible (Seely 1978, Walter 1986) - this means that we find distinct temporal variation. But even in the E Sahara with a (averaged) precipitation of 1 mm/yr (or even less) the following observation could be made: The main part of the area under question is characterized by (Nubian) sandstone and other cristalline rock, interrupted by some granitic outcrops. But in one place, close to Six Hills, a limestone hill occurs. Here in the fissures of the rock remains of a seed plant (*Fagonia* sp.) could be detected (see Fig. 2).

The examples show that for a better understanding of the phenomenon it seems necessary to look closer to the definition of allochthonous ecosystems.1) A seed or fruit, i.e. a diaspore, is just a life stage of green plant, and is a hint for potential vegetation growth. In a completely allochthonous ecosystem no diaspore bank should be available. 2) In almost all ecosystems photosynthetic carbon gain and respiratory carbon consumption go hand in hand. Odum (1959) calls plant communities autotrophic if the ratio of photosynthetic production (P) to respiratory consumption (R) is >1, but heterotrophic if P: R < 1. In the latter case the ecosystems receive to a smaller or larger extent carbon imput from outside, they are at least partially carbon allochthonous. In completely allochthonous ecosystems the P: R ratio is zero

These two conditions will exclude ecosystems with short- or mid-term temporal variation. But still the problem of spatial variation exists because a pattern of completely allochthonous and only partially allochthonous ecosystems usually is developed in the same region. In order to come to a proper delineation we have to look to the surrounding ecosystems and to the transition zones. This will be done using the example of the E Sahara.

Accidental vegetation

Fig. 2 shows in the very center a large area which is completely free of vegetation (the limestone hill, signature D, has already been mentioned above as an exception). The central part, which as a landscape ecological unit has been called "extreme desert III" by Bornkamm & Kehl (1990), is surrounded to the W and N by a small belt of *Stipagrostis acutiflora* as only species as first vegetation zone. Similar as in the following zone with *Salsola imbricata* and *Fagonia* sp. the vast majority of the individuals is dead, only very few living specimens can be found at a time, and mostly the specimens and stands or their remains are located at great distances (up to several tenths of km) from each other. Precipitation events can be expected in intervals of several decades, and will take place very locally. The vegetation is triggered by these rains and lasts as long as water is available in the soil. This type of vegetation has been called "accidental vegetation" by Kassas (1952), the relevant landscape ecological unit has been called "extreme desert II" by Bornkamm & Kehl (1990). The accidental vegetation seems to be the most widespread type of vegetation in the Western Desert of Egypt (Kassas 1971).

The outermost parts of the accidental vegetation are extremely scarce. Nevertheless the ecosystem is not completely allochthonous any more for two reasons: A diaspore bank is available, and primary productivity exists. The productivity, however, is still close to zero. Bornkamm (1987 b) computed the necromass of a stand consisting in three tussocks of *Stipagrostis acutiflora* as 0.07 t dry matter / ha. This equals the production during the year when the stand has been built up. Taking into account the probability of rainfalls only every 25-50 years, the productivity expressed in t / ha × a would be even much lower.

The example mentioned is located in a large serir area in the Western Desert where

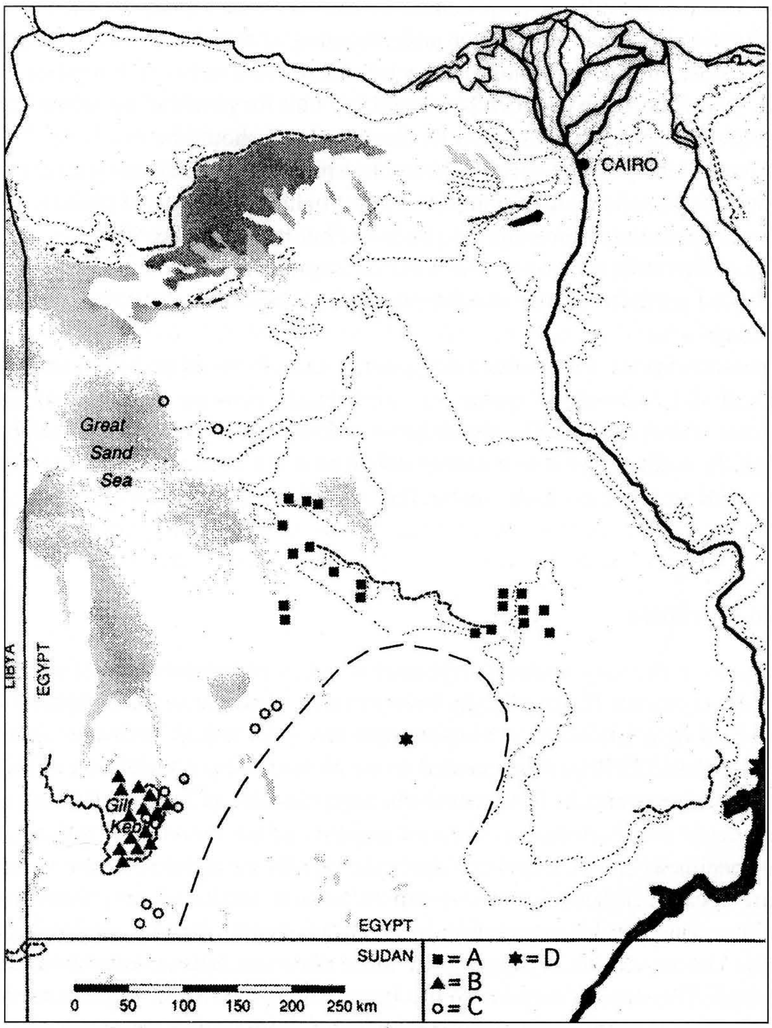

Fig. 2. Distribution of ecosystem types and vegetation in SW Egypt. Allochthonous ecosystems, free of vegetation: inside broken line; autochthonous ecosystems, accidental vegetation: A *Zygophyllum coccineum* - *Salsola baryosma* - ass., B monospecific *Salsola baryosma* stands, C monospecific *Stipagrostis acutiflora* stands, D remains of stands of *Fagonia* sp.

redistribution of precipitated water does not take place. The situation changes when run-off water is available. Springuel & al. (1990) established permanent plots in Wadi Aggag close to Aswan in the Eastern Desert. Here the average precipitation is around 5 mm / a and, according to the hilly character of the area, floods arise after every storm which may happen once or twice within 10 years. One of the groups of permanent plots shall be discussed here as a good example of accidental vegetation.

Fig. 3 shows a cross section of Wadi Aggag along the line where the permanent plots are located. Here strong storms occurred at the end of 1996 which destroyed all former vegetation with the exception of one small tree of *Acacia ehrenbergiana* which, however, was bent down by the flood. The cross section was recorded one year after the event, in November 1997. Each sector of the cross section was 3 m wide and 8.3 m long (= 25 m^2 in total). The valley shows an asymmetric shape with a flat N-facing slope (left) and a steeper S-facing slope (right).

The surface of the N-facing slope is mainly made up of granite boulders and sand, the central part of sand and gravel, the S-facing slope of bare rocks and boulders. In the marginal parts of the transect plant density, species richness and especially cover were lower than in central parts, and all plants were dead already. In the central parts 30 - 100 % of the individuals were living and provided 70 - 100 % of the total cover. This means that the surviving specimens were larger than the dead ones. Minimum values in sector 9 indicate that here the destructive effect of the flood was strongest. Hight was measured only with the living individuals. The mean values for height in Fig. 3 increased from to N in the central part of the valley and indicated that the moisture conditions were most favourable in sector 12. This is probably due to the fact that here bare rock covers the surface with the result that water penetrates rapidly and deeply into the soil.

Both examples show clearly that the accidental vegetation is very much triggered by the water conditions and has to start again and again after the rare precipitation events.

Life forms

The third and last problem to be discussed are the life forms involved in the transition zone between completely allochthonous ecosystems and ecosystems bearing at least some producers. Kassas (1952) stated already that the plants of the accidental vegetation do not fit into the categories of life forms under more regular rainfall conditions like annuals or perennials. We have seen that the emergence of the species in the accidental vegetation is rain-triggered and that the life cycle is determined by the availability of water, i.e. both the beginning of growth and the extension of the life cycle are not caused by biological traits but by an environmental factor. Haines (1951) coined the term "potential annuals" for species which usually exhibit perennial growth but also can come into flower vigorously already in the first year. He established a sequence of species (Fig. 4) from species with a strong tendency to a short life cycle to species which tend more to longer life cycles up to species that never will flower in the first year - like *Acacia tortilis*! For some of them it would be possible to say that they mostly perform a short life cycle under the conditions given but can live longer if conditions allow and, thus, can be called "potential perennials" (Bornkamm & Kehl 1990).

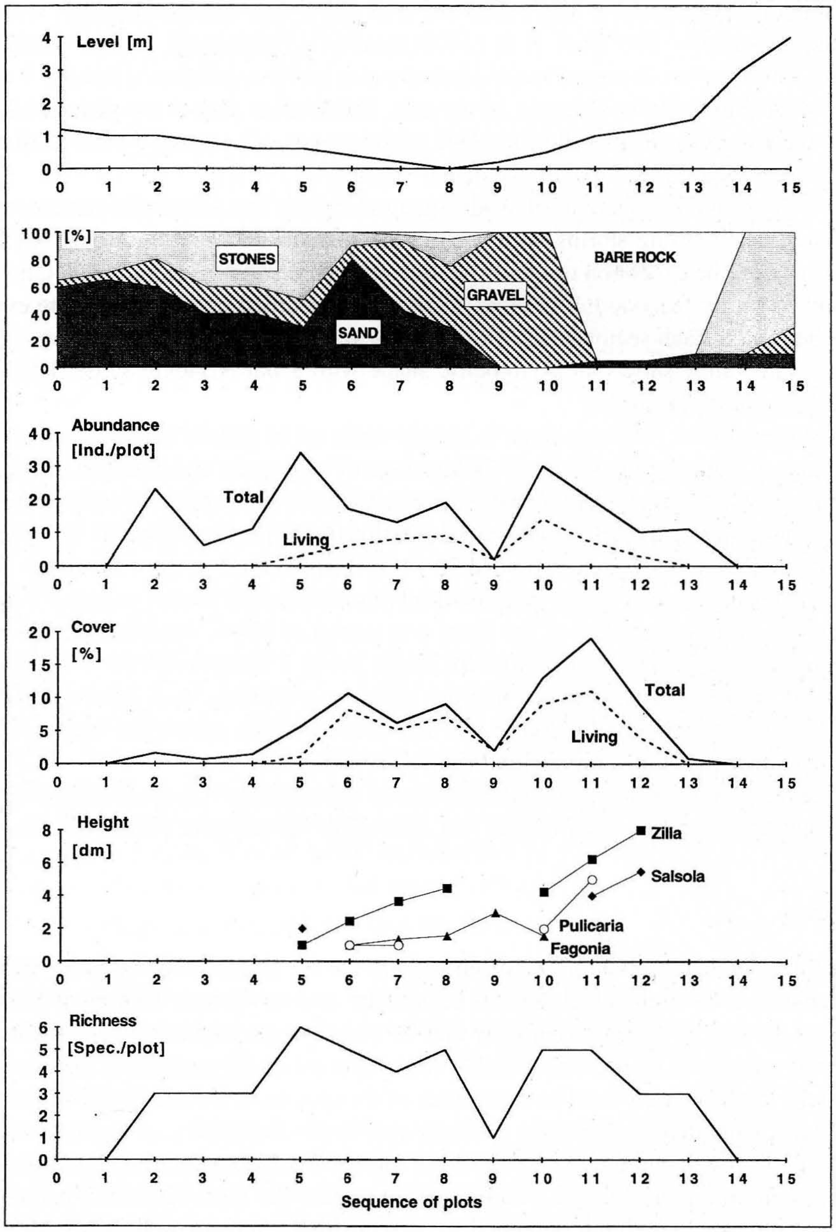

Fig. 3. Transect through the downstream part of Wadi Aggag NE of Aswan, Egypt, from S (left) to N (right). Size of plots (sectors) 8,3 m long, 3 m wide, 25 sqm area. From above to below: Height in m above the lowest point (estimated); surface cover in % of the area, stones = boulders + stones, gravel = gravel + coarse sand; abundance = plant individuals per plot; cover = plant cover per plot; mean height of living individuals in the plot (in dm) for *Zilla spinosa, Salsola imbricata, Pulicaria crispa & incisa* and *Fagonia indica & bruguieri;* species richness = number of species per plot.

SPECIES NAME	TENDENCY TO FLOWER IN THE FIRST YEAR
DIPLOTAXIS ACRIS	ALWAYS (TRUE ANNUAL)
DIPLOTAXIS HARRA	VERY FREQUENTLY
CAYLUSEA HEXAGYNA	REGULARLY
FARSETIA AEGYPTIA	LESS IMPORTANT
ZILLA SPINOSA	INCIDENTAL
ACACIA TORTILIS	NEVER (TRUE PERENNIAL)

Fig. 4. List from Haines (1951) for explanation of the "potential annuals" as a life form between true annuals and true perennials.

Both terms are not satisfying. The species under question are certainly not annuals (and likewise not therophytes) because an annual growth rhythm does not exist. And the term "perennial" does not apply because the growth can be stopped at any time by exhaustion of the water reserves. For this reason they do not fit into the system of life forms worked out by Ellenberg & Mueller-Dombois (1967). Looking for a better term it has to be taken into account that they share with the therophytes an obligatory diaspore bank and the survival of unfavourable periods in form of diaspores; and they share with the perennials the occasional presence of a bud bank. In our second example some of them like *Morettia philaeana* show a tendency to the first group mentioned, others like *Zilla spinosa, Salsola imbricata, Fagonia arabica, F. bruguieri,* and *Pulicaria crispa, P. incisa* show a tendency more to second group. Since they all have in common that their periodicity is variable and is biased by an external factor I would call them poikilorhythmic species.

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